

be physical space; for example, overlap between species – in all other resource dimensions – can occur if there is spatial differentiation of the “realized” niches (Cunha and Vieira 2004). Yet if resource use and resource overlap among animals are not considered in all three spatial dimensions simultaneously, then characterization of the spatial aspect of resource use will be inadequate (WebFigure 1d). Spatial differentiation among species is often achieved through differential use of vertical space (eg MacArthur 1958), in combination with inherent differentiation among available resources (such as food and nest sites) along the vertical dimension. Therefore, quantification of 3D space use can improve our understanding of resource use and spatial overlap or differentiation by species. For instance, consider the seminal work by MacArthur (1958); resource partitioning among ecologically similar species could be placed in a 3D context, with volumes of space assigned a probability of occupancy for each species based on resource attributes and ecological constraints (ie competitors; WebFigure 1d).

Probabilistic estimation of 3D space use will also be invaluable for addressing numerous conservation and societal issues, including some involving human health and safety. For example, bird strikes with aircraft cost worldwide civil aviation >US\$1.2 billion annually (Allan 2002). Currently we are investigating approaches for predicting 3D space use by birds to assess associated aviation risks, which will provide information to wildlife managers on how to reduce the likelihood of strikes. Similar quantification of organisms’ 3D space use could be integrated into wind farm planning efforts to mitigate associated bird, bat, and insect mortality. Likewise, knowing the spatial distributions of target and non-target marine organisms could be used to optimize timing and location of harvest to reduce fisheries bycatch.

An important practical limitation in implementing these ideas is the “curse of dimensionality”; overall data

requirements necessary for appropriate inference increase by at least one order of magnitude for each additional dimension of interest (Silverman 1986). However, current technology for tracking animals allows today’s researchers to collect large amounts of data accurately and to pursue these fundamental ecological and applied questions for many species. During the past decade, there has been an explosion of technological advancements, dramatically improving the ability to assess multi-dimensional space use, examine mechanisms driving resource-use patterns, and understand the causes of observed use (Cooke *et al.* 2004), including reduced size and cost, and increased availability of Global Positioning System transmitters; increased locational accuracy from acoustic and other tags (eg Melnychuk and Christensen 2009); and advanced integration of sensors recording vertical space use (eg Moll *et al.* 2007). Furthermore, remote sensing technologies (eg light detection and ranging [LiDAR]) that characterize above-ground structure with more accuracy and precision will assist in quantifying habitat use in 3D space. However, although modern technology may be of enormous benefit in many situations, simple field observations (eg MacArthur 1958) can often still provide the necessary data for development of models summarizing multi-dimensional space use.

We are approaching the next frontier in advancing our understanding of multi-dimensional space use. This understanding is critical for better assessing theoretical and applied questions that have long been of importance to ecologists. The appropriate data-gathering technologies are now available. What remains is the challenge of integrating and applying them to answer those questions.

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Is assisted colonization feasible? Lessons from past introductions

Assisted colonization – or the translocation of species to previously unoccupied ranges predicted to be favorable for persistence under future climate scenarios (hereafter AC) – has been proposed for addressing

extinction risk of climate-imperiled species, and is hotly debated because of associated uncertainties, such as the risk of translocated species becoming invasive (eg Loss *et al.* 2011; Thomas 2011). Here, we focus on factors limiting its applicability and potential risks for target species overlooked by both AC advocates and opponents (Hewitt *et al.* 2011).

Deliberate introductions of alien species have similarities with AC; through a comparative framework, examining the former may help to identify some of the latter's constraints and predict its success, despite inherent differences between traits of introduced alien and imperiled species (Blackburn and Jeschke 2009). A large proportion of deliberate introductions of alien species failed across taxa and regions, with establishment success depending in part on species-specific traits, biotic and abiotic conditions of the recipient region, and complex interactions between them (eg Blackburn *et al.* 2009). Regarding AC of climate-imperiled species, abiotic conditions of source and recipient areas should match future – not present – conditions. Current models of the climate–biosphere interface remain overly simplistic, however, thereby undermining the credibility of projections (McMahon *et al.* 2011) and complicating the selection of appropriate recipient areas. Although substantial progress in modeling could soon be made, which would improve our predictive ability (McMahon *et al.* 2011), AC is proposed as a method of last resort to prevent the extinction of climate-imperiled species. Consequently, what would be the establishment likelihood for species translocated decades before recipient regions are predicted to be climatically suitable (surely much lower than that resulting from alien species' introductions matching native to non-native conditions)?

In addition, propagule size and number are key determinants of establishment success of alien species (Simberloff 2009); the more individ-

uals per introduction and the more introductions altogether, the more likely those introduced species are to become established. Indeed, much uncertainty exists about propagule pressure thresholds to guarantee successful alien establishments, given the magnitude of variance among species and introduction events (Simberloff 2009). Variance was also pronounced when reviewing the success of reintroduction of species within portions of their former range, although Griffith *et al.* (1989) found that successful programs released, on average, more animals than unsuccessful ones (160 as compared with 54, respectively). Taking this into account, is it advisable to translocate a sufficient number of wild-caught animals, as recommended by Hewitt *et al.* (2011), to ensure successful AC, given that highly imperiled species often have global population sizes of only a few hundred individuals? Paradoxically, AC could increase extinction risk of remnant native populations for the sake of obtaining large enough propagule sizes.

Clearly such problems would not be affiliated with organisms from which seeds or gametes could be stored or frozen until suitable AC sites could be found (Vitt *et al.* 2010). There is, however, an additional challenge related to genetics. Surprisingly, alien species introductions were apparently not compromised by the expected low genetic variability of small founder populations (Simberloff 2009); introduced alien species commonly have large native populations and widespread distributions (Blackburn and Jeschke 2009), thus ensuring genetic variability. By way of comparison, imperiled species often exhibit restricted ranges, depleted population sizes, and low genetic variability, likely symptomatic of their inability to keep pace evolutionarily with severe anthropogenic threats (Kinnison and Hairston 2007). Indeed, reintroduction success of endangered species is half that of more common

species (Griffith *et al.* 1989). Therefore, the diminished genetic potential of imperiled species to face new selective forces in recipient areas might seriously compromise AC success.

In a changing world driven by anthropogenic forces, we feel that controversial actions such as AC must be seriously considered. However, potential risks affecting the viability of AC and target species should be further debated and incorporated into decision-making frameworks (Loss *et al.* 2011) before action is taken.

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